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the black feathers of the breast which are untouched. The black and naked barbs shown in Fig. 2 give that portion of the breast its hairy or bristly appearance.

An effort to assign a cause for this peculiar habit of the Sage Cock would be entering the purely speculative field, but the sliding of the widely distended air sacks over an uneven surface, together with the additional rumbling produced by the stiffened worn-off feathers, undoubtedly produce, to the ears of the bird at least, a volume of sound that is simply tremendous. A spectator, however, can hear nothing until the air sacks are collapsed.



'APTOSOCHROMATISM.'

BY J. A. ALLEN.

IN 'Science' of Feb. 23, 1900 (N. S., XI, pp. 292-299) Mr. F. J. Birtwell describes at considerable length, what he considers a case of 'The Occurrence of Aptosochromatism in *Passerina cyanea*.' He says: "The following remarks upon Aptosochromatism of *Passerina cyanea*, although of insufficient importance to establish the phenomenon of color change without moult as a constant occurrence in the species, are conclusive enough, I am convinced, to prove the possibility of such a change, and are merely offered as such for what they may be worth." Several paragraphs, by way of introduction, relate to the general subject, in which Mr. Birtwell regrets that "Individual error and dogmatism have greatly retarded honest effort in this most important branch of ornithological science. It is a singular fact that certain individuals have conceived the idea that a feather once having passed its premature condition is utterly disconnected with the vital system of the bird, and such individuals cling to this belief with a tenacity wonderful to behold." His remarks, he tells us, "are based chiefly upon observations conducted during the fall, winter, and early spring of 1898-99, upon a captive bird." He presents a table

showing loss of feathers from Nov. 1 to Feb. 11, and adds that from Feb. 11 to Feb. 28 "an average of 50 contour feathers was lost daily," and that "the loss had abruptly ceased" by March 5. (The bird died March 29.) The total loss of contour feathers was estimated at 1350, or about three-fifths of the bird's entire plumage. He says: "To many observers my bird by March 5th would have been pronounced to be completely moulting." This feather loss he does not consider as normal, but as resulting indirectly from the bird's timid, fretful temperament, many of his feathers becoming more or less injured by his "wild fluttering" in the cage, and consequently shed, as, "when such a vital process as Aptosochromatism [with a big A] begins to work, these decrepit feathers necessarily would have to be renewed in order to take part in the general plan. . . . It will be noticed in the table how gradually the loss began, due doubtless to the gradual approach of activity towards color change in the feathers. It must be admitted that this explanation is purely hypothetical, but such a hypothesis, although not of fundamental importance, oft-times prepares the way for a clearer understanding of the problem under consideration."

"The first appearances of color change," he says, "were noticed in some of the old feathers of the crown during the first week in February," when "a brightening of the blue area of the feather was noticed, but no perceptible change of color at the tips where the russet was. . . . When the band of tawny was reached, it appeared to be slowly absorbed until but faint tips of this color could be seen upon the ends of the larger barbs. In no cases were the barbs or barbules broken off sufficiently to account for the change." After describing the general course and character of the color change over the body Mr. Birtwell sums up as follows: "While my bird threw out no hint whatever as to the constant occurrence of the color change, it did prove that the 'impossibility' is possible. It is certain that the heavy feather loss of my bird but indirectly helped the change: 1st, we have seen that many feathers changed which were not renewed by moult; 2d, we saw that those feathers which were renewed by direct gain and loss were colored similarly to those which preceded them, but that later on they changed Aptosochromatically, and 3d, no purely blue, *i. e.*,

changed feathers were found in an embryonic condition at any time, although frequent careful examinations of the bird were made." This, as will be noted later, is, taken altogether, a fine exposé of Mr. Birtwell's ignorance of what normally occurs in respect to color change without moult, or by simple normal abrasion. He goes on to say that in feathers examined under the microscope in January and February he "could detect no presence of carrier pigment cells and found the calamus of each feather to be in the expected dried up condition. The change would thus seem to be confined to activity¹ in the feathers alone." (!)

His conclusions from this study are: "(1) that Aptosochromatism in my *Passerina cyanea* occurred beyond doubt, (2) that although present with severe feather loss it does not follow that the gain of color was directly responsible to it, as proved by careful examination of the newly acquired feathers, and (3) that although the feather loss was objectively independent of the Aptosochromatic change, it might subjectively be so, inasmuch as old and imperfect feathers were renewed for active and healthy ones, in which such a color change subsequently occurred."

Dr. J. Dwight, Jr., in a later number of 'Science' (April 30, 1900, pp. 627-630), under the title 'The Plumage and Moults of the Indigo Bunting,' reviews Mr. Birtwell's paper at some length, describing in detail the successive stages of plumage of this bird, and criticising with some sharpness the class of work Mr. Birtwell's paper so characteristically illustrates. After quoting some of Mr. Birtwell's comments on the attitude of the opponents of the theory of 'Aptosochromatism,' transcribed at the beginning of this review, in which he says "they cling to their belief with a tenacity wonderful to behold," Dr. Dwight says: "Doubtless it does seem 'wonderful' to persons who would wave aside all the careful observations that have been made upon feather growth and feather wear, and plumage generally, but possibly it is not so wonderful as the strange things they see just as soon as they watch a bird of striking colors in a cage." Dr. Dwight also indulges in some comment on the general subject. After his account of the changes of plumage in the Indigo Bunting, he says: "Here then we have the facts about the Indigo Bunting, and any

specimens taken at the proper time of year will verify them. Nevertheless, Mr. Birtwell thinks that 'for good results in investigations upon color change one should operate rather upon live birds in confinement.' Well, perhaps so, for the 'proof' of color change without moult certainly does rest chiefly upon caged birds. The fact that they moult irregularly and often at long intervals and, as for instance in the Purple Finch (*Carpodacus purpureus*), having once lost their bright colors may never regain them does not seem to impair belief in a theory fifty years or more old. It began when most people were ignorant of the fact that birds could and did moult twice in the year. This was sagely declared to be too great a drain upon their vitality; but when it was found that some species did moult twice, theory had to be reserved for others that did not appear to be guilty of draining their vitality. When these in turn were proved to moult twice refuge was taken in the assumption that only certain individuals of certain species changed color without moult. Later came red-handed proof of guilt in feathers found growing upon these individuals and the believers in theory fell back upon the claim that although one feather did seem to be renewed by moult, the one next to it underwent a color change, concerning the nature of which no two believers were agreed. Some of them have gone so far as to assert rejuvenation of frayed edges by some sort of exudative processes which only need to be carried a step farther to eliminate altogether the necessity of moult. This is no fancy picture and I only paint it that my readers may know what 'aptosochromatism' represents."

Referring more directly to Mr. Birtwell's article, Dr. Dwight remarks: "An observer who did not know the plumage differences between the adult and the young bird, nor discover the structural differences between autumnal and nuptial feathers, nor hesitate to look for 'carrier pigment cells' under the microscope, may well have his accuracy of observation questioned. . . . When the well-established laws of feather growth and feather loss fail to account for plumages, it will be time enough to adopt theories demanding new life in epidermal structures, that for many months have been histologically dead. The existence of such a thing as 'aptosochromatism' will hardly be proved by those who have no

grasp upon fundamental principles, and as long as such observers expect to be taken seriously, they must not be surprised if they are called sharply to account."

A careful study of Mr. Birtwell's paper has convinced me that there is nothing very unusual about Mr. Birtwell's caged Indigo Bunting. No 'hypothesis' is necessary to account for its moulting at the time it did, nor would Mr. Birtwell have thought any 'hypothesis' necessary if he had known the simple facts that the species normally moults twice a year, and that the prenuptial moult is ordinarily more or less incomplete. Nor is there anything in the color changes described incompatible with the belief that the changes observed were wholly due to the normal shedding of the tips of the feathers, both in the new feathers and in the old ones. The gradual wearing off of the tips of the feathers necessarily results in the exposure more and more of the previously concealed blue basal portion of the feathers underneath them, which would result in "the apparent brightening of the blue portion of the feather, beginning evenly on each vane from the bottom," as remarked by Mr. Birtwell. He further says: "When the band of tawny was reached, it appeared slowly to be absorbed until but faint tips of this color could be seen upon the ends of the larger barbs." Here almost certainly Mr. Birtwell's observations were in error, as he could easily have himself detected had he been familiar with the differences in structure between the fugacious buffy tip and the main body of the feather; although he gives it as his opinion that "in no case were the barbs or barbules broken off sufficiently to account for the change." There is nothing to indicate that Mr. Birtwell's bird was not a male of probably the second (possibly of the previous) year undergoing (1) the normal spring moult of the species and (2) gradually changing color, in case of both the old plumage and the new, by the usual wearing away of the fugacious brown feather tips and gradually exposing more and more of the previously concealed basal portions of the feathers, as occurs normally, to a greater or less extent, in hundreds of species of our birds, and so markedly in such species as the Snowflake, Bobolink, and many others that might be mentioned.

Mr. J. Lewis Bonhote has also shown of late much interest in

'aptosochromatism'; but, perhaps to his credit, is content with the more commonplace phrase 'colour-change' to designate "an alteration or rearrangement of pigment in the fully-grown feather," including as well "an influx of pigment into a fully formed feather." In 'The Zoölogist' for January, 1900 (pp. 29-31), he has a paper 'On the Moulting and Colour Changes of the Corn-crake (*Crex pratensis*)," in which he points out that "the Corn-crake undergoes a complete moult in spring, the new dress resembling its winter plumage." He adds that "the slate-colour of the breeding-dress is, however, assumed immediately after the moult by a *change of colour*!" In a later paper, published in 'The Ibis' for July, 1900 (pp. 464-474), entitled 'On Moulting and Colour-change in Birds,' he again refers to the Corn-crake, and cites this case as disproving the widely entertained belief that 'colour-change' relieves "the severer strain on the system" caused by moult since in this species there is both a spring moult and a 'colour-change.'

The paper just cited is called forth, Mr. Bonhote tells us, by "three recent papers on the subject which have appeared in American periodicals," these being (1) Dr. Chadbourne's in 'The Auk' (XIV, 1897, pp. 137-149) on the 'Spring Plumage of the Bobolink'; (2) a paper by the present writer published in 1896 (Bull. Am. Mus. Nat. Hist. VIII, pp. 13-44), entitled 'Alleged Changes of Color in the Feathers of Birds without Molting'; and (3) Mr. Witmer Stone's paper in the Proceedings of the Academy of Natural Sciences of Philadelphia (1896, pp. 108-167), on 'The Molting of Birds with Special Reference to the Plumages of the Smaller Land Birds of Eastern North America.' Mr. Bonhote, being an 'aptosochromatist,' finds much in Dr. Chadbourne's paper to approve, while the other two articles are made the subject of considerable adverse criticism. With regard to Mr. Stone's paper it is pointed out that it is incomplete, inasmuch as "the Limicolæ and Gamebirds have been left untouched." As Mr. Bonhote has considerable to say about some of the former, as the Ruff and the Golden Plover, it seems a little strange that he does not mention Mr. Chapman's paper on 'The Changes of Plumage in the Dunlin and Sanderling,' which immediately precedes in the same volume (Bull. Am. Mus. Nat. Hist., VIII, 1896, pp. 9-12) one of the papers to which he devotes attention.

Apropos of Dr. Chadbourne's paper on the Bobolink, Mr. Bonhote says: "The Bobolink is not the only bird in which the assumption of the breeding plumage varies in different individuals. From the head of *Larus ridibundus* I have taken at the same time new brown feathers and old feathers in process of change, while in other individuals *there has been a pure colour-change*. The Ruff is an instance of the change going on in *two different ways simultaneously*. The Ptarmigan, again, is another instance, and from the examples of this species which I have examined I think it doubtful whether it assumes any one of its plumages in a uniform manner. The fact that a bird will assume its breeding plumage in some feathers by a change of colour, and in others by a change of feather, *leads to the supposition* that pigment *can* find its way up an old and fully-grown feather. It does not seem to me unlikely that, at a certain season, pigment — which is chiefly a waste product, more abundant, on account of the extra energy expended, at the approach of spring — should be deposited in the follicles of the feathers. If the follicle is at that time engaged in producing a *new* feather, the pigment is placed in it; if not, *it is drawn up into the feather which is already full grown*!"

This quotation shows fairly Mr. Bonhote's position. Respecting the portions here placed in italic type, I beg to offer a few words of comment. First, as to the *Larus ridibundus*, it seems strange that I have never been able to detect, in any of the large number of specimens I have examined of its closely allied congeners, any "old feathers in process of change," but always, in birds taken at the proper season, plenty of new black feathers in all stages of growth. As to the Ptarmigan, I would call Dr. Bonhote's attention to Dr. Dwight's paper in the April number of this Journal, published before Mr. Bonhote's paper appeared. Dr. Dwight's whole article on 'The Moults of the North American Tetraonidæ' (Auk, XIII, 1900, pp. 34-51, 143-166), I hope will be not only read, but most critically studied by all who share Mr. Bonhote's views on 'colour-change.' Says Dr. Dwight (*l. c.*, pp. 147, 149): "The study of this material [just previously enumerated], amounting to nearly two hundred specimens, now enables me to explain the parti-colored plumages of these birds, a matter that has long baffled investigation and given rise to a belief

that individual feathers themselves change color without being moulted. It has been believed by some that Ptarmigans moult continuously and in a haphazard way during the whole year. All of these ideas have arisen from a misconception of the facts, which show that the feathers supposed to be changing color or pattern are of that particular color and pattern at the time they first expand, and that the continuous moult resolves itself into definite periods, and that the feather growth is systematic, differing in no respect from that of the rest of the Grouse. The one essential difference between the moults of the Ptarmigans and those of the Grouse is found in the extra moult in the autumn by which the brown feathers regularly assumed at the usual periods of moult in both young birds and old are replaced by white ones.

"The plumages of the Ptarmigans are puzzling not only on account of the plumage intermediate between summer and winter dress, but also on account of the rapidity with which the moults follow each other, one beginning before the previous one is completed, and apparently overlapping at some points. Moreover, the incompleteness of the partial moults with the irregular retention of feathers peculiar to them adds to the confusion of ideas resulting from seeing together an assemblage of feathers belonging to several different stages of plumage. As for the rapidity with which one moult treads upon the heels of another, it can only be said that the mode of life of the Ptarmigans requires it and the activity of the feather papilla is no greater than the necessity. As a matter of fact, some papillæ produce approximately one feather in May, another in July and a third in September, but there are many which produce but two feathers during this period and others only one, while all of them are dormant during the long winters."

In respect to "the supposition that pigment *can* find its way up an old and fully-grown feather," Mr. Bonhote assumes that this supposition is true, and that, in the season of moult, "if the follicle [of a feather] is at that time engaged in producing a *new* feather, the pigment is placed in it; if not, *it is drawn up into the feather which is already full-grown.*" This latter affirmation, put forth as a statement of known fact, rests entirely upon a series of

wholly inadequate assumptions, namely: (1) the case of the Golden Plover, in which he says, "if a specimen be examined in spring, we find the white feathers on the breast in all stages of colour between white and black. Messrs. Allen and Stone would have us believe that these are all new feathers, which have grown of that colour, and which will always remain of that colour." In summer Mr. Bonhote finds that the "many birds in the full summer dress" that he has examined rarely have "more than one or two feathers in this half-and-half stage on any single individual." The conclusion reached is that the Golden Plover assumes the breeding dress "by direct moult" on the back while it acquires its black breast by the white feathers *turning black*. "The new growing feathers on the breast," he says, "are *white*, not black or particoloured, and then change to the black summer dress." I cannot say from personal observation what the European Golden Plover does, but the American Golden Plover and its near ally, the Black-breasted Plover, acquire the black breast feathers by a moult, as the examination of a large number of specimens has abundantly shown.¹ (2) As to the physiological process involved in this change of white feathers to black ones, Mr. Bonhote says: "I am not in a position to write about it at present, but should like to draw attention to a paper by M. V. Fatio, in which he shows that an oil is continually making its way into the feather from the body." As "most pigments are soluble in ether, alcohol, or chloroform," they are thus proved "to be of an oily nature. Now, if it has been proved that oil can make its way up a feather, and, further, that all true pigments (black, red, and their combinations) are of an oily nature, it necessarily follows that pigment can make its way up also." Yet it is admitted "that this flow is not due to any active agent, but to osmosis, capillarity, or some similar action"! We know the results of capillarity; its action is evident as a mechanical process in a thousand ways. But what has this to do, we may ask, with the

¹ Since this article was sent to the printer we have received the manuscript of Dr. Dwight's important paper, given later in this number of 'The Auk,' on the 'Moult of the North American Shore Birds (Limicolæ),' to which the reader's attention is especially called in reference to the Golden and Black-bellied Plovers.

(1) secretion of pigment by the vital action of a pigment secreting organ, and (2) the transmission of the pigment through the structure of a fully matured feather, and hence (according to the best histologists) a histologically dead organ. Because an oil or a dye can diffuse itself through a skein of yarn or over the external surface of a feather, and possibly penetrate its porous structure, Mr. Bonhote claims that such experiments "clearly prove that it is quite possible for pigment deposited at the *base of a feather* [just where and in what manner?] to work its way up by *purely physical means*. If an artificial pigment can do this, we need have no doubt that it is possible for a natural pigment to do the same."

Here, then, is the whole basis of the theory of 'color-change' in feathers, or 'aptosochromatism,' as set forth by one of its latest supporters; an assumption to my mind, resting: (1) on erroneous observation, and (2) on conjecture of what may or ought to happen if this belief in 'colour-change' were true. Victor Fatio's above cited observations and conclusions, published a generation ago, need not awaken much surprise, but it is a matter for astonishment that they should find supporters in this closing year of the nineteenth century.

Since Mr. Bonhote finds that I have "adduced no proofs in favour of non-colour change" in my paper on this subject published in 1896, it is hardly worth while to discuss the subject further in the present connection. In view of such a statement, however, I can hardly believe that my critic has given the paper in question very careful attention. As the subject is at present receiving renewed consideration, I am quite willing to await the results of expert investigators in this special line of research, both from the histological side and from the standpoint of the student of moult and plumage change in general. As Dr. Dwight, who has already spent years in the study of this subject, has well said: "When the well-established laws of feather growth and feather loss fail to account for plumages, it will be time to adopt theories demanding new life in epidermal structures, that for many months have been histologically dead."